Effect of mate size on maternal reproductive effort in the convict cichlid *Amatitlania siquia*

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Abstract   The differential allocation hypothesis predicts individuals will increase their reproductive investment when mated to a high quality partner. In many species of fish with biparental care females prefer large males due to the males' greater ability to raise more offspring to independence. I examined the relationship between mate quality, parental care and number of offspring in a natural population of convict cichlids *Amatitlania siquia*. The frequency of frontal displays by females was positively correlated with male standard length. Additionally, as males increased in length relative to their mate, females increased the frequency of chases towards predators, while males decreased the number of displays towards brood predators. This trade-off in parental effort within a pair due to mate quality is a key prediction of differential allocation. The number of offspring was correlated with male, but not female, standard length. These results support the differential allocation hypothesis in that females offered more parental care to offspring of a larger male, while their mates decreased the amount of care they provided. Additionally, females benefited in terms of number of offspring by pairing with higher quality mates. Increased female investment may provide an incentive to ensure male care and maintain pair bonding, which could lead to greater reproductive success through increased offspring survival [*Current Zoology* 58 (1): 66–72, 2012].

Keywords   Differential allocation, Biparental care, Maternal effort, Cichlid

In species with biparental care, where the quality of a partner influences offspring quality and/or number, either sex may alter its parental investment depending on the quality of its mate. The differential allocation hypothesis (DAH) predicts individuals will increase the amount of care they provide to progeny when mated to a high quality partner (Burley, 1986). It was initially formulated for species exhibiting biparental care where the additional care provided to offspring served as an incentive to maintain pair-bonding (Burley, 1988). It predicts that the less attractive partner will increase its care while its attractive mate will decrease its investment (Burley, 1986). The anticipated quality of future partners and the degree to which mate quality affects offspring survival are factors expected to influence degrees of differential allocation (Sheldon, 2000).

While parental care occurs in only 20% of all fish families (Blumer, 1982), all of the currently recognized species of cichlids (family: Cichlidae) exhibit either uniparental or biparental care (Keenleyside, 1991). The unique feature of ubiquitous care makes cichlids an excellent taxon in which to investigate patterns of differential allocation. Many species of cichlids practice biparental care to combat intense predation of fry (Perrone

and Zaret, 1979), making Burley's (1986) focus on the role of differential allocation in maintaining pair bonds applicable.

In many Neotropical cichlids with biparental care large males are preferred mates due to their greater ability to secure preferred spawning sites (Perrone, 1978; Itzkowitz et al., 1998) and protect offspring (Wisenden, 1994b; Gagliardi-Seeley and Itzkowitz, 2006). However, desertion by males has been reported in several species (*Amatitlania siquia*, Wisenden, 1994a; *Aequidens coeruleopunctatus*, Jennions and Polakow, 2001; *Amphilophus sagittae* and *A. zaliosus*, Lehtonen et al., 2011) with male-deserted broods containing fewer offspring (Wisenden, 1994a) and smaller young (Lehtonen et al., 2011) than non-deserted broods. The direct positive effect of the male's presence on both the number of offspring and growth rate are reasons for females to increase the amount of care they provide if it ensures their mate stays. Hypothetically, females could balance the cost of increased parental investment with the benefit of increased offspring survival if it decreased the likelihood of abandonment of broods by males.

Convict cichlids *Amatitlania siquia* range from Guatemala to Panama, inhabiting lakes and streams (Bus-

sing, 1987). They are a sequentially monogamous species exhibiting biparental care. Upon pair formation a male and female will excavate a cave where the eggs are then laid. The offspring become free-swimming fry approximately a week after hatching and emerge from the cave at 4.5-5 mm in standard length (tip of the snout to the posterior end of the caudal peduncle). The offspring become independent after approximately six weeks, at which point the pair bond between the parents is terminated. Despite both sexes preferring larger individuals as mates (Noonan, 1983; Beeching and Hopp, 1999), mutual mate choice (Beeching and Hopp, 1999) results in small males pairing with small females and large males obtaining large females as partners (McKaye, 1986). Males are almost always larger than females within pairs (McKaye, 1986), with females on average 13.2 mm smaller than their mates (Wisenden, 1995). However, there is considerable variation in the pattern of size-assortative mating, with females mating with males 1 mm smaller or up to 31 mm larger than themselves (Wisenden, 1995). A consequence of the assortative size-based pattern is that the attractiveness of an individual is a function of its mate's size. A small female would be less likely to obtain a large male due to the size assortative mating; this would therefore result in a large male being of greater quality to a small female than to a large female. The short-term nature of the pair bond and the variation in size of mate a female obtains make convict cichlids an ideal organism in which to study how mate quality influences the investment decisions in a single reproductive cycle.

The purpose of this study was to investigate patterns of parental investment in a natural population of convict cichlids and to determine if there was a relationship between mate quality and level of parental care provided by both parents of a breeding pair. I predicted that if a relationship was found females would increase their investment when mated to a high quality male. Due to the direct benefits large males provide to the offspring and the assortative size-based mating pattern, high quality males are large males and males that are substantially larger than their partners. The prediction of altered investment due to mate quality is consistent with the DAH in which individuals increase their parental investment when mated to a more attractive partner.

1 Material and Methods

The study was conducted in the río Cabuyo within Lomas de Barbudal Biological Reserve, Guanacaste, Costa Rica (10º30'N, 85º22'W) during February–March 2011. Lomas de Barbudal is located within a tropical dry forest and the study was conducted during the dry season. The site is a series of shallow, connected pools approximately 250 m in total length.

Reproductive pairs were located during snorkeling surveys and uniquely identified using their location within the stream, size of the fry, and distinguishing marks (scars, torn fins, etc) on the parents. Subsequent to each pair and fry sighting, a 10-minute behavioral observation was conducted using a mask and snorkel. A pair of observers simultaneously recorded six discrete behaviors of both parents: 1) chases (rapidly swimming at a predator), 2) biting (making contact with the predator), 3) frontal display (flaring the opercula while facing the predator), 4) fin digging/leaf turning (agitating the substrate or turning leaves over to provide food for offspring), 5) time away from the brood (more than 3 body lengths), and 6) frequency of foraging (feeding without spitting food out that offspring could eat). The frequency of chases has been used in previous field studies of convict cichlids (Wisenden, 1994b; Snekser et al., 2011) and the other behaviors have been utilized in field and laboratory studies of convict cichlids (Lavery and Keenleyside, 1990; Lavery, 1995; Wisenden, 2008). At the end of the observation period the fry were captured using a combination of aquarium hand nets and a 30-ml plastic pipette. A countable number of fry (between 5 and 10) were left with the parents to ensure they did not leave the area. The captured fry were placed in an 8-liter bucket. The plastic pipette was used to siphon fry into a smaller container for counting and the standard lengths (SL) of the first 10 fry were measured. The fry would typically form a school within the bucket so individual fry were not singled out for measuring. After processing, the fry were placed in a clear container (21.6 cm × 10.2 cm × 9.5 cm). The container was lowered into the water and inverted once it was within approximately 10 cm of the remaining fry. The fry within the container would swim out and the parents would resume defense behavior of the returned fry.

On the next day that the site was surveyed (between one and four days later) previously observed pairs were located. A second 10-minute behavioral observation was conducted using the same behavioral parameters from the first observation. After the observation was completed the parents and offspring were captured. A 6-m seine net with 3.2 cm² mesh was used to surround the fish. The male was captured first using a small aquarium net. Next, all the fry were captured using a combination of hand nets and a 30-ml plastic pipette. The female was

caught last, with the same method used to capture the male.

Eight-liter buckets were used to separate and temporarily house the parents from the fry. Adults were anesthetized using Aqui-S (Aqui-S New Zealand Ltd.) and marked with a unique combination of visible elastomer implant (Northwest Marine Technologies) along the dorsal area. Adults were weighed and the SL measured. A small portion of the caudal fin was removed for genetic sampling. The adults were then placed in an aerated bucket (Penn-Plax Silent Air® B11) to recover from the anesthetic. While the adults recovered, the fry were processed in an identical manner as on the first observation date. The SL of the first 10 fry siphoned into the smaller container was measured and the remaining fry tallied. After the adults had recovered from the anesthetic, parents and offspring were housed in the same bucket. The bucket was placed within the confines of the net at the original capture site and lowered into the water. The adults would swim out and the fry would follow them out of the bucket and settle on the substrate. After the fish left the bucket the net was removed.

Data were analyzed in JMP 9 (SAS Institute, Cary, NC). Linear regressions were used to analyze the effects of male SL, female SL, intra-pair size difference (male SL-female SL), and all interaction terms on parental behavior for both sexes. Forward inclusion and backward elimination was used to exclude non-significant terms from analysis of each behavior. Once models included only significant terms, repeated measures analysis of variances (ANOVAs) were used with significant model effects as the between-subject variable and observation date as the within-subject treatment. Repeated measures ANOVAs were used in case there were changes in an individual's behavior between the first and second observation. Linear regression was used to determine the relationship between parental standard lengths and number of observed offspring. The number of offspring at the first observation date was used in case possible handling effects affected the number of offspring at the second observation date. Values are reported as the mean ± standard error (*SE*).

2　Results

2.1　Size of breeding pairs

There was a significant positive size-assortative mating pattern ($F_{1, 28}$=18.44, *P*=0.0002; Fig. 1). Males were larger than their partners in all pairs, with a mean intra-pair size difference of 21.5 ± 4.66 mm (Table 1). The largest female was smaller in standard length than the
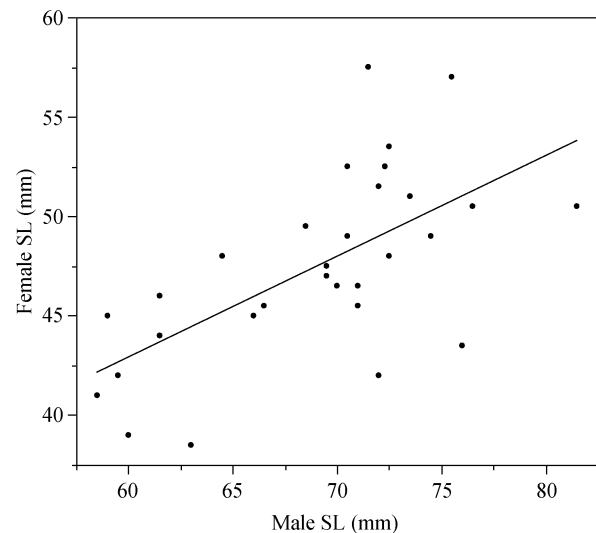

Fig. 1　Correlation between male standard length and female standard length for breeding pairs (Y=0.51X + 12.56, r^2=0.375)

Table 1　Standard lengths (mm) of breeding male and female convict cichlids

	Mean	*SE*	Min	Max	*n*
Male SL	69.0	1.06	58.5	81.5	30
Female SL	47.5	0.86	38.5	57.5	30
Intra-pair difference (M-F)	21.5	4.66	14	32.5	30

smallest male sampled (Table 1).

2.2　Female parental behavior

The frequency of female bites, fin dig/leaf turn, foraging or time away was not significantly correlated with any of the model effects. Intra-pair size difference was the best predictor of female chase frequency. Frequency of chases by females was positively related to the intra-pair size difference ($F_{1, 28}$=9.37, *P*=0.0048; Fig. 2). Male SL was ranked as the best predictor of female frontal display frequency ($F_{1, 25}$=0.68, *P*=0.0004), and female displays were positively related to male SL. The interaction effect of male SL and female SL on frequency of female displays was also significant ($F_{1, 25}$=0.60, *P*=0.0007), indicating that as male SL increased large females increased their frequency of frontal displays.

2.3　Male parental behavior

The frequency of male chases, bites, fin dig/leaf turn, foraging or time away was not significantly correlated with any of the model effects. Intra-pair size difference was the best predictor of male frontal display frequency. Males performed significantly fewer frontal displays as
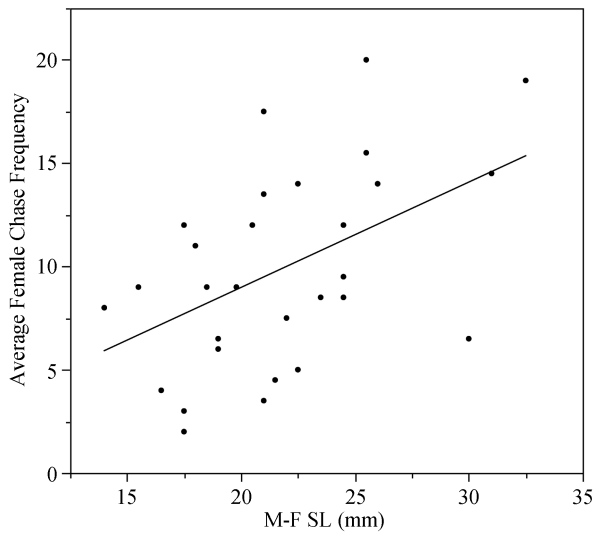
Fig. 2 Correlation between intra-pair size difference and average female chase frequency per 10-minute observation ($Y=0.51X - 1.22$, $r^2=0.224$)

An average of the two observations was used since within-subject variation was non-significant ($F_{1, 28}=0.0002$, $P=0.9389$).
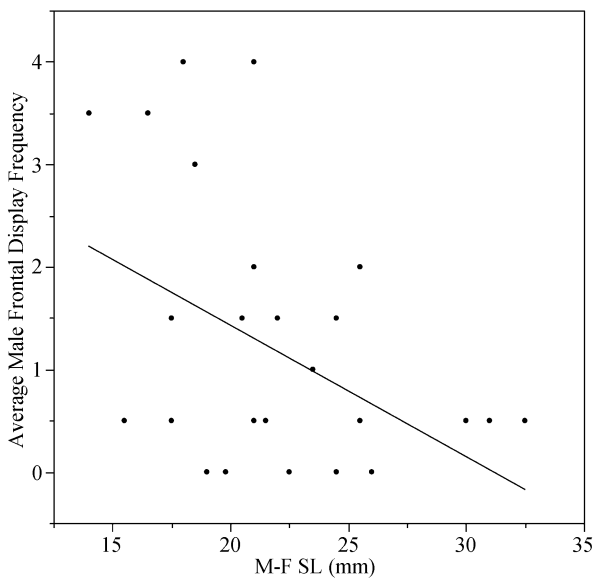

Fig. 3 Correlation between intra-pair size difference and average male frontal display frequency per 10-minute observation ($Y= -0.13X + 3.99$, $r^2=0.169$)

An average of the two observations was used since within-subject variation was non-significant ($F_{1, 28}=0.02$, $P=0.424$).

the intra-pair size difference increased ($F_{1, 28}=6.88$, $P=0.014$, Fig. 3).

2.4 Number of offspring

The mean number of offspring at the first observation date was 61.6 ± 6.27, with a range from 17–140 ($n = 30$). The intra-pair size difference was not correlated with the number of offspring at the first observation ($F_{1, 28}=3.02$, $P=0.093$), nor was female SL ($F_{1, 28}=0.854$, $P=0.363$). However, male SL was positively correlated with the number of fry at the first observation ($F_{1, 28}=4.91$, $P=0.035$; Fig. 4).
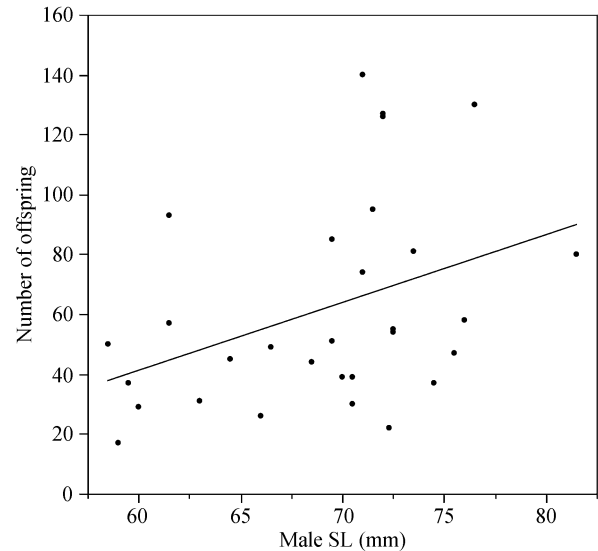

Fig. 4 Correlation between male standard length and number of offspring at the first observation ($Y=2.27X - 94.76$, $r^2=0.119$)

3 Discussion

Females performed significantly more chases towards potential brood predators as the intra-pair size difference increased. Females also performed more frontal displays when mated to large males. The significant interaction effect of male SL and female SL for female frontal displays could indicate that females also take into consideration their own size when determining the most effective tactic against a potential brood predator. As males increased in size relative to their partner they decreased their parental effort in the form of frontal displays. These results are consistent with the differential allocation hypothesis (DAH, Burley, 1986), which predicts that the less attractive mate will increase its parental effort while its more attractive partner will decrease its effort. It is thought that the increase in effort by the unattractive mate serves as an incentive to maintain the pair bond between the parents. The average chase frequency for all females was 9.7 ± 0.87 and for all males was 6.3 ± 0.71 per 10-minute observation. This is similar to a previous study conducted on a natural population of convict cichlids that found female chase frequency to be 13.84 ± 1.33 and male chase frequency was 7.29 ± 0.93 per 10-minute observation

(Wisenden, 1994b).

The four other observed behaviors (biting, leaf turning/fin digging, foraging, and time spent away from the brood) were not significantly correlated with mate quality. For a parent to bite a potential brood predator the likelihood of injury to the parent itself would be greater than if it chased or displayed from a safe distance. Parents, as well as offspring, were observed feeding on the detritus found on the overturned leaves. The behavior may benefit the parents as much as the offspring and thus should not be correlated with the quality of an individual's mate. The observance of parents feeding on the overturned leaves could also explain why a correlation between foraging and mate quality was not found. The offspring are more vulnerable when a parent spends time away from the brood since only one parent is left guarding. Male SL is positively correlated with the number of offspring at independence (Wisenden, 1994b) and solitary females of a closely related species, *Amphilophus sagittae*, guard significantly smaller territories (Lehtonen et al., 2011). If large males spent more time away, the smaller parent would be left alone to guard which could impact defense effectiveness and the number of offspring that reach independence.

The number of offspring at the first observation date was correlated with male SL. Previous research has observed positive relationships between male size and offspring survival in convict cichlids (Wisenden, 1994a; Gagliardi-Seeley and Itzkowitz, 2006). The benefit of increased offspring survival likely outweighs the costs of increased brood defense by the female, making differential allocation an adaptive strategy.

The parental compensation theory also attempts to explain why differences in parental effort within a pair occurs and predicts that when one parent reduces its parental contribution its partner will increase its effort in an attempt to compensate (Wright and Cuthill, 1989). Compensation by one parent in response to a reduction in care offered by its mate has been observed in both birds and fish with biparental care (*Sturnus vulgaris*, Wright and Cuthill, 1990; *Eretmodus cyanostictus*, Steinegger and Taborsky, 2007). The positive correlation between female defense behavior and male quality and negative correlation between male defense behavior and intra-pair size difference could indicate that females were compensating for a reduction in their partners' parental effort instead of increasing their effort due to a higher quality mate. However, the parental compensation hypothesis does not predict how the quality of an

individual or its partner should influence adjustment of effort in response to a reduction in parental contribution. Parental care is likely to be energetically more expensive for smaller individuals of both sexes since increased defensive behavior reduces energetic reserves (Steinhart et al., 2005). As reproductive potential is tightly correlated with somatic reserves in fish (Gross and Sargent, 1985), increased energetic expenditures to compensate for its partner's reduced effort could impact future breeding success. When considering the impact of reduced future reproductive potential, a negative relationship between female parental effort and male quality would be expected. This is because small females, those likely to have the largest difference in size with their partners, should conserve energy to minimize the impact on future reproduction. Larger males should increase their energetic investment to compensate for reduced efforts by smaller females. Small males should also be expected to exhibit a lower level of care compared to larger males, which would predict a positive relationship between male defense behavior and intra-pair size difference. This prediction for how an individual's size would affect the parental compensation theory is the opposite of the observed pattern in this study in which smaller males and females had the highest level of parental care.

A surprising finding of this study was that male, but not female, SL was positively correlated with the number of offspring. In fish there is a positive correlation between female size and fecundity (Gross and Sargent, 1985), and this pattern has been found during laboratory experiments involving convict cichlids (Galvani and Coleman, 1998). The results of this study indicate that the protective assistance of males may be crucial for offspring survival, and male size may instead be a better predictor of the number of offspring produced for a particular reproductive bout. By mating with larger males females may gain a direct benefit in terms of young produced. Previous field observations in convict cichlids have found evidence for the protective abilities of large males; Gagliardi-Seeley and Itzkowitz (2006) observed fewer intruders near the offspring of large males, while Wisenden (1994b) found that the number of offspring at independence was positively correlated with male SL. An alternative hypothesis for the relationship between male size and the number of offspring is that females increase the number of eggs they produce for a larger mate. This would also support the DAH with females not only increasing their secondary reproductive effort in the form of parental care but also their primary

effort. Increased primary reproductive effort either in increased egg number (Côte and Hunte, 1989; Skinner and Watt, 2007; Evans et al., 2010) or size (Kolm, 2001) has been found in fish for females mated to preferred or more attractive males. The pattern of females increasing egg number or egg size for preferred males has only been investigated in fish with either no parental care (Evans et al., 2010) or male-only care (Kolm, 2001). Since female convict cichlids must also maintain enough energetic reserves to provide extended parental care the ability to increase egg number may be more limited.

In summary, this study found a correlation between mate quality and the amount of parental care in breeding pairs of convict cichlids. Females were observed to increase their parental effort while males decreased their investment as male quality increased. This study is the first example of increased parental care in a fish in response to mate quality. This suggests that differential allocation is likely to be utilized by a range of taxa to increase reproductive success when a high quality mate is obtained. The aim of future research should include investigating female fecundity in relation to male quality. This will help clarify how females balance the two components that contribute to parental investment during a reproductive event. If females increase fecundity and also provide a greater proportion of the parental care they may incur greater reductions in future reproductive potential. If the benefit from increased investment for an attractive mate is sufficient to offset a reduction in future reproduction, differential allocation should result in a greater number of offspring produced for a female compared to an individual that does not adjust its investment. Increased female investment may provide an incentive to maintain pair bonding with males, which could increase offspring survival, and ultimately contribute to greater reproductive success.

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